

# DEVONIAN MIOSPORE ASSEMBLAGES FROM FAIR ISLE, SHETLAND

by J. E. A. MARSHALL and K. C. ALLEN

**ABSTRACT.** Miospore assemblages have been isolated from a Devonian sequence of Old Red Sandstone facies, on Fair Isle, Shetland. The special problems encountered in processing these palynomorphs with their high carbonization levels and subsequent darkening are mentioned. Thirty miospore species are recorded and their taxonomic problems and stratigraphical significance are discussed. Comparisons with similar assemblages from the northern hemisphere indicate a Givetian (in parts specifically late Givetian) age for the Fair Isle material. The genus *Rhabdosporites* Richardson 1960 is emended, and *R. langii* Richardson 1960 and *R. parvulus* Richardson 1965 are combined. The ecological significance of *Geminspora* (Balme) Owens 1971 is discussed.

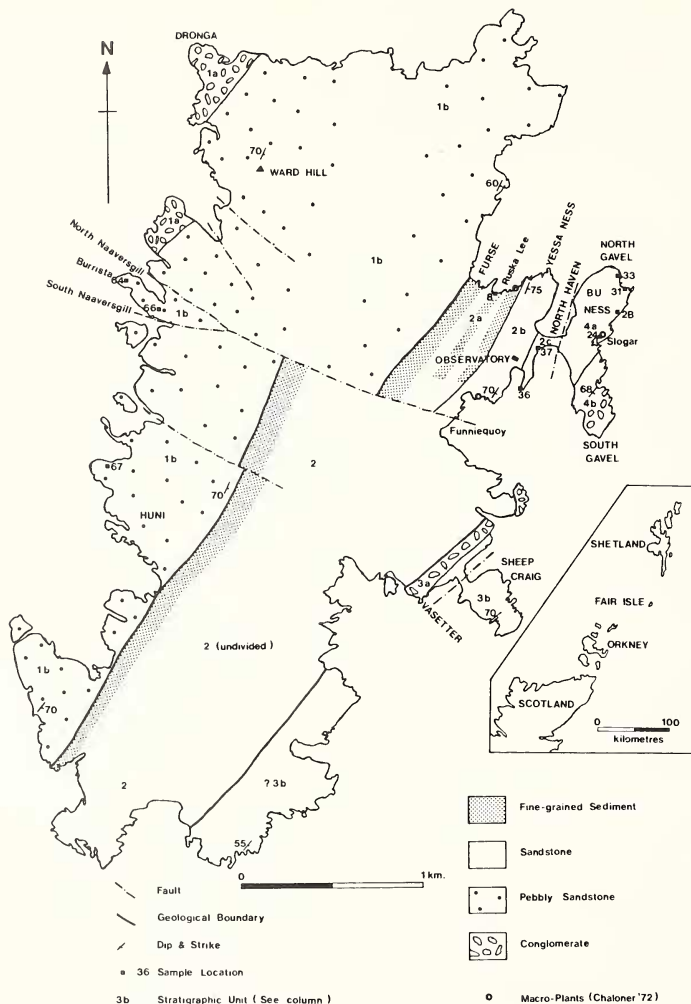
SHETLAND contains one of the most complex set of continental Devonian rocks in Britain, with different rock sequences juxtaposed by major transcurrent faults. These complex structural relationships have proved very difficult to elucidate, and this has not been helped by the poor biostratigraphic control between the different basins. It is hoped that palynological contributions will give the biostratigraphic basis for a comparison of the time relations in these sedimentary basins, and will yield information on the timing of the movements along the major transcurrent faults, about which there is still much controversy (Smith 1977). This paper deals with the sequence found in the small (5 km × 3 km), isolated Devonian outlier of Fair Isle, which lies 39 km south-west of the southern tip of mainland Shetland (text-fig. 1). Emphasis is placed on stratigraphic palynology; little attempt has been made to formally modify, or add to existing taxonomy. This is because of serious preservational problems encountered in the palynological studies, which are discussed later.

## THE DEVONIAN SUCCESSION ON FAIR ISLE

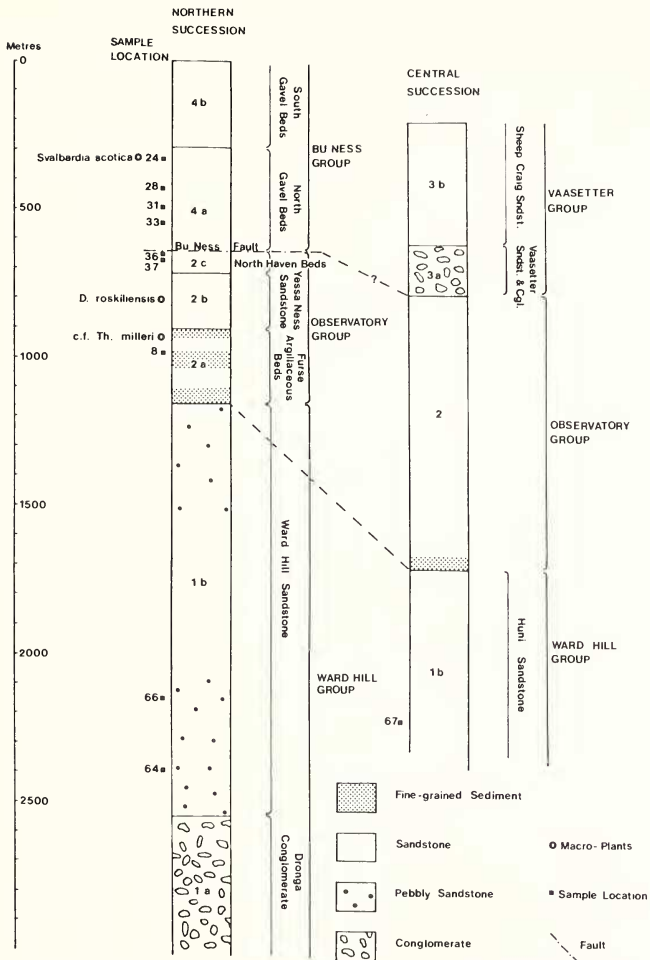
Although Fair Isle has a relatively small Devonian outcrop, its geographical position (text-fig. 1) is of importance because it is generally considered (Mykura and Young 1969; Mykura 1972a) to lie just to the east of the Walls Boundary Fault, which is a possible extension of the Great Glen Fault. It has also been suggested (Mykura 1976; Donovan, Archer, Turner, and Tarling 1976) that it is part of the same sedimentary basin as that in which the Walls Sandstone was deposited, and movements along this fault have placed it in its present position. Any indication therefore of the precise age could help clarify these palaeogeographic relationships.

The most recent and complete accounts of the geology of Fair Isle are those of Mykura (1972a, 1972b, 1976), and this brief synopsis is drawn from them. The Fair Isle sedimentary sequence (for which neither the top nor the base is seen), is composed of over 3000 m of dominantly clastic terrigenous sediments, all steeply dipping east-south-east. The rocks have been subdivided (Mykura's nomenclature and notation followed here) into four stratigraphic subdivisions (see text-figs. 1, 2), on the basis of lithological differences. These units can be traced with varying degrees of accuracy across the island, but the presence of two major east-north-east trending faults create local correlation difficulties which are only partially solved by lithological mapping.

The lowest unit is the Ward Hill Group (1a and 1b in Mykura's notation), composed of over 1600 m of conglomerates and sandstones. This is succeeded by the Observatory Group (2a, 2b, and 2c) with over 900 m of sandstones and finer sediments including dolomitic siltstones and mudstones. Above this, the Vaasetter Group (3a and 3b) which is only exposed in the central fault block, is composed of about 600 m of conglomerates and sandstones, most of which are inaccessible. The top



TEXT-FIG. 1. Geological map of Fair Isle (after Mykura), showing location of palynological samples and plant macrofossil sites.



TEXT-FIG. 2. Stratigraphical section of Fair Isle (after Mykura) showing position of palynological samples.

unit, the Bu Ness Group (4a and 4b), consists of approximately 600 m of conglomerates, sandstones, and siltstones; is seen only in the northern succession of the island where it is faulted against the Observatory Group (2a, 2b, and 2c).

Increasing tectonic disturbance is seen in the rocks towards the southern end of the island where they exhibit prominent cleavage, minor folding, mineralization, and the emplacement of small dyke intrusions. The cause of this disturbance has been discussed by Mykura (1972*a*) who suggested a possible granitic intrusion lying off the south-east coast of the island.

Previous palaeontological records are very restricted, and largely limited to the plant macrofossil remains described by Chaloner (1972), for which the localities are shown on text-fig. 1. The fossil plants clearly indicate a Devonian age. Chaloner tentatively suggests an age not older than middle Siegenian for the Observatory Group (Unit 2a) based on the presence of *Dawsonites roskiliensis* Chaloner 1972, and an age not older than Eifelian, but more likely Middle Devonian, for the Bu Ness Group (Unit 4a), based on the occurrence of *Svalbardia scotica* Chaloner 1972. Other plants include cf. *Thursophyton milleri* (Salter) Nathorst 1915 in the Observatory Group and hostinellid axes and cf. *Prototaxites* Dawson 1859 in the Bu Ness Group.

The Bu Ness Group yields the only animal fossils yet found, which include dipnoan scales, an arthrodire plate (?*Cocosteus* Agassiz 1844) and the branchiopod *Asmussia* Pacht, 1849. These also favour a Middle Devonian age for this group.

#### MATERIAL AND METHODS

Four samples were initially provided by the Institute of Geological Sciences (Edinburgh), and when two of these were found to contain miospores a field trip was made to the island, and seventy-eight samples were collected from fine-grained dark-grey to black clastic rocks for palynological analysis. Of these, sixty-one were processed, but only ten gave assemblages of sufficient quantity and preservation to merit further study. The best-preserved assemblages were from the Observatory Group; followed by the Bu Ness and Ward Hill Groups. Very poor preservation was found in the argillaceous units (2a) of the Furse Argillaceous Beds where there was some cleavage development. The lack of miospores in the southern part of the island is of interest, as it is in accord with the increased deformation reported by Mykura (1972*a*). Megaspores were also rare and usually fragmentary. This can be related to the orthogonal crack sets seen on some of the larger specimens, which may result from an incipient cleavage (or shrinkage), causing their fragmentation during deformation or in the processing (Burmman 1969).

The samples were firstly demineralized with hydrochloric and hydrofluoric acids, then screen-washed through a twenty micron nylon sieve, before being cleaned of insoluble fluorides with repeated hot HCl treatments to give a kerogen concentrate. The miospore assemblages were very highly carbonized (black in colour), and the only oxidizing medium found capable of clearing them was a fuming Schulze mixture. The oxidations were carried out in a porosity-2 sinter funnel/buchner flask system linked with a low-pressure air line to give continuous aeration (Neves and Dale 1963). The Schulze mixture was made up with fuming nitric acid either at full strength or freshly diluted with water, but always at a concentration greater than 70%. The time taken for the miospores to be oxidized to a level suitable for transmitted light microscopy varied from 5 to 30 minutes. In addition, a marked preferential clearing was seen, with some of the thicker walled (e.g. *Hystricosporites* spp.) miospores never attaining more than a low level of translucency. Samples from different horizons showed very different oxidation characteristics. Those from the Furse Argillaceous Beds (2a), required only 5 minutes' oxidation time and a relatively weak fuming Schulze, to reveal a poorly preserved assemblage; whilst samples from the Bu Ness Group needed stronger and longer oxidation, but gave much better-preserved assemblages.

After oxidation the miospores showed the phenomenon of redarkening (to opacity) in 1 to 3 days, with the thicker-walled miospores deteriorating much more rapidly. This degradation was accelerated by heating and water removal, so that an inert non-water miscible plastic mounting medium could not be used, as dehydration was impossible under normal conditions. Silicone oil was



also tried, but the dehydration step involving tertiary butyl alcohol, produced a rapid darkening reaction in the cleared sample. Eventually, glycerol jelly was used as the mounting medium, and this gave assemblages which could be studied for up to 3 days. The breakdown and darkening of the exines when mounted in glycerol jelly was noticeable, with degradational products imparting a yellow stain to the mounting medium. Miospores with thicker exines (e.g. *Hystricosporites*, *Geminospora*) showed a more rapid return to opacity, and had to be studied during the first day.

A subsequent study of palynological assemblages from the Devonian of the south-east mainland of Shetland also showed this oxidation problem. There, it was much more serious, with viability times of about 5 minutes in glycerol jelly. During this time the miospores could be seen to redarken and start to dissolve. It was then that a special technique was developed which involved a matching of the oxidizing media strength to a miospore assemblage preservation, and the use of a rapid drying technique which dehydrated the miospores faster than they could redarken, so that an inert plastic mountant could be used (Marshall 1980).

The assemblages from Fair Isle were all studied from repeated oxidation, with fresh assemblage slides being made up every 2 to 3 days. The study was therefore limited by the amount of organic residue per sample; some giving enough material for seventy to eighty slides, others only having sufficient for four or five. All the slides have been kept, and co-ordinates given for illustrated specimens in the event that advances in techniques, such as infra-red microscopy, will enable palynomorphs to be studied without further recourse to oxidative clearing.

One difficulty in dealing with such highly carbonized assemblages ('vitrinite' reflectance measurements from Fair Isle give values of approx. 4 to 5%, pers. comm. Dr. J. M. Jones), is that the identification of reworked components by colour differences is not possible. Three species are described (*Emphanisporites rotatus*, *Camptozonotriletes aliquantus*, and *Grandispora ?naumovii*) which occur in a very low proportion, and it is possible that these may represent reworked components (see Clayton, Higgs, and Keegan 1977 for a discussion of *Emphanisporites*). However, until one is better able to recognize features of reworking such as breakage and erosion (as in Birks 1970), both this possibility and that of their continued presence as minor and rare elements in the flora must be considered.

#### PREVIOUS PALYNOLOGICAL STUDIES FROM SHETLAND AND ADJACENT AREAS

The pioneer work on Old Red Sandstone palynology in Britain was carried out by Lang (1925) as part of his study of the Orcadian Basin flora. Later, Richardson produced a series of papers (1960, 1962, 1965) on the classical Orcadian area. Since then, very little work has been published except for brief taxonomic lists as, for example, Donovan, Collins, Rowlands, and Archer (1978), who give an account of a miospore assemblage from the island of Foula (western Shetland). Two doctoral theses have included a certain amount of Orcadian palynology. Fannin (1970), in conjunction with Richardson, has tabulated information on the palaeoecology and stratigraphic distribution of miospore assemblages from Orkney, whilst Fletcher (1976) studied the megaspores of the Melby Fish Beds. Although a useful amount of data has accumulated on the taxonomy of Devonian spores from the Orcadian Basin, very little is known of their detailed stratigraphic distribution, and this has been a major handicap to any precise correlation.

#### STATISTICS AND DATA HANDLING

The treatment of the simple bivariate statistical data, such as the exoexine and intexine diameters of miospores, presents problems for data handling and statistical testing. Classical regression analysis is not applicable, as there are no dependent and independent variates; furthermore, there is no easy solution to fit a best line to this type of two-error data. Various iterative methods such as those described by Williamson (1968), York (1966), and comparatively reviewed by Brooks, Hart, and Wendt (1972),

demand statistical estimates for the variances of each data point. These are certainly not worth the extra time involved for the quality of data produced on the Fair Isle material. An approximate method is the Reduced Major Axis line as described by Kermack and Haldane (1950), and further documented by Till (1974) and others. The statistical validity of the line produced is in doubt, but as it appears correct (i.e. passes through the centre of the experimental scatter), it is a useful means of comparing populations, providing not too much reliance is placed on any subsequent statistical tests based upon it.

The data in the bivariate plots were in fact computed for logarithmic and linear fits, using both classical regression and the reduced major axis line to find the best fit. The latter was found to be more successful in describing a line through a set of data points. However, the logarithmic fit did not give much advantage over the linear model. When data values were taken from published graphical plots (Richardson 1965), an electronic digitizing machine (D-MAC) was used to provide more accurate results and known estimates of error.

#### NOMENCLATURE AND SYSTEMATICS

The morphological terminology used is that of Smith and Butterworth (1967), and their classification system is followed except for the inclusion of *Hystricosporites*, *Ancyrospora*, and *Geminospora* in an *incertae sedis* group, following the practice of Strel (in Becker, Bless, Strel, and Thorez 1974). No categories higher than infraturmae are used, and the retusoid miospores are retained in the *Laevigati* and *Apiculati*, because haplotypic features are not here regarded as being of major classificatory importance.

Figured material is housed in the palaeobotanical collection of the Department of Botany, Bristol University. Co-ordinates given refer to a Leitz Orthoplan microscope no. 715334. A ringed reference slide is also provided. Each sample number (i.e. Fair 66) is followed by a strew slide number and then the appropriate co-ordinates.

Infraturma LAEVIGATI Bennie and Kidston emend. Potonić and Kremp 1954

Genus TRILEITES Erdtman ex Potonić 1956

*Type species. Trileites spurius* Dijkstra emend. Potonić 1956

*Trileites langii* Richardson 1965

Plate 30, fig. 1

*Dimensions* (two specimens). Maximum equatorial diameters 141 and 160  $\mu\text{m}$ .

*Lithostratigraphic Range.* Ward Hill Sandstone (1b); sample Fair 66 (see text-fig. 2).

#### EXPLANATION OF PLATE 30

All figures  $\times 400$  unless otherwise stated.

Fig. 1. *Trileites langii* Richardson 1965. Fair 66.2, 48.9, 98.7

Figs. 2, 5. *Acinosporites lindlarensis* Riegel 1968 var. *minor* McGregor and Camfield 1976. Fair 37.80, 37.4, 104.8,  $\times 1000$  Distal and proximal surfaces respectively.

Figs. 3, 4. *Camptozonotriletes aliquantus* Allen 1965. 3, Distal view. 4,  $\times 1000$  Distal surface showing sculpture. Both Fair 66.2, 17.5, 109.8

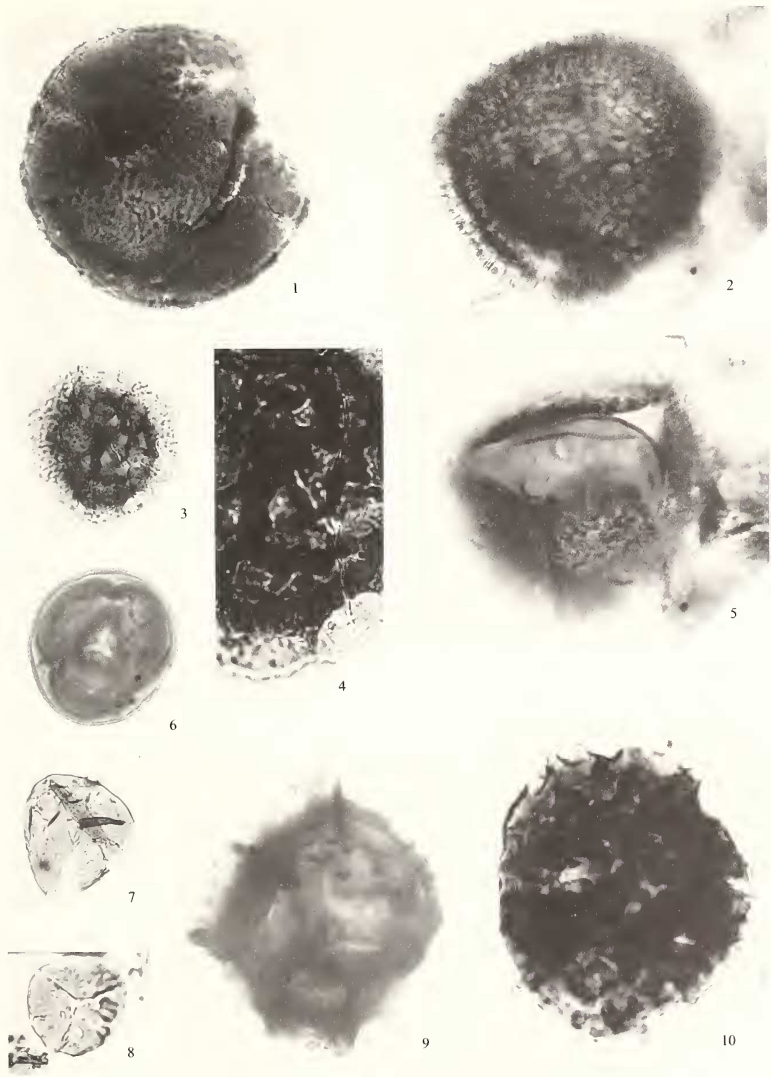
Fig. 6. *Retusotriletes rotundus* (Strel) Lele and Strel 1969. Fair 37.79, 19.9, 106.0.

Fig. 7. *Calamospora atava* (Naumova) McGregor 1964. Fair 37.79, 26.9, 96.5

Fig. 8. *Emphanisporites rotatus* (McGregor) McGregor 1973. Fair 28.32, 114.6, 27.2

Fig. 9. *Chelinospora concinna* Allen 1965.  $\times 1000$ . Fair 37.1, 25.9, 115.3

Fig. 10. *Convolutispora disparalis* Allen 1965.  $\times 1000$  Fair 24.40, 50.0, 100.3



MARSHALL and ALLEN, Devonian miospores

*Remarks.* Similar to the population described by Richardson (1965), but smaller in over-all diameter. However, it is comparable with the miospores described by Chi and Hills (1976), and is here referred to *Trileites langii*.

Genus *RETUSOTRILETES* Naumova 1953 emend. StreeI 1964

*Type species.* *Retusotriletes simplex* Naumova 1953

*Retusotriletes rotundus* (StreeI) Lele and StreeI 1969

Plate 30, fig. 6

Synonymy, see McGregor (1973, p. 20).

*Dimensions* (eighteen specimens). Maximum equatorial diameter 56–80  $\mu\text{m}$  (mean 67  $\mu\text{m}$ ).

*Lithostratigraphic range.* Ward Hill, Observatory, and Bu Ness Groups (1b to 4a). Found in all samples examined.

*Remarks.* This is an example from the wide variety of retusoid forms which occur in the Fair Isle assemblages.

Genus *CALAMOSPORA* Schopf, Wilson, and Bentall 1944

*Type species.* *Calamospora hartungiana* Schopf, Wilson, and Bentall 1944

*Calamospora atava* (Naumova) McGregor 1964

Plate 30, fig. 7

*Dimensions* (twenty-four specimens). Maximum equatorial diameter 27–71  $\mu\text{m}$  (mean 56  $\mu\text{m}$ ).

*Lithostratigraphic range.* Ward Hill Group to Bu Ness Group (1b to 4a). In all samples examined except Fair 33 (see text-fig. 2).

*Remarks.* Compares well with the emended species described by McGregor (1964), but exhibits a slightly greater size range.

Infraturma *MURORNATI* Potonić and Kremp 1954

Genus *CONVULUTISPORA* Hoffmeister, Staplin, and Malloy 1955

*Type species.* *Convolutispora florida* Hoffmeister, Staplin, and Malloy 1955

*Convolutispora disparalis* Allen 1965

Plate 30, fig. 10

*Dimensions* (six specimens). Maximum equatorial diameter 36–54  $\mu\text{m}$  (mean 46  $\mu\text{m}$ ).

*Lithostratigraphic range.* Bu Ness Group (4a); samples Fair 24 and 28.

*Remarks.* As stated in Allen (1965) it is thought likely that sculptural elements of this type result from corrosion of the exine. It is noticeable that a wide range of sculpture is present, with transitional forms resembling *Raistrickia* Potonić and Kremp 1954.

Genus *EMPHANISPORITES* McGregor 1961

*Type species.* *Emphanisporites rotatus* McGregor 1961

*Emphanisporites rotatus* McGregor emend. McGregor 1973

Plate 30, fig. 8

Synonymy, see McGregor (1973, p. 46).

*Dimensions* (three specimens). Maximum equatorial diameter 33, 38, and 50  $\mu\text{m}$ .*Lithostratigraphic range*. Observatory and Bu Ness Groups (4a and 2c); samples Fair 28 and 37.*Remarks*. Clayton *et al.* (1977) have documented a series of sporadic occurrences of *Emphanisporites* spp. from the later Devonian and early Carboniferous of southern Ireland. Similar sporadic occurrences were also noted by Richardson (1965) from the Eday Flags of the Orcadian Basin. It seems likely that the Fair Isle occurrences are only rare examples of a minor but persistent element in the flora. The decision when to regard elements of an assemblage as reworked or rare is often difficult (see *Captozonotrilites aliquantus*), and should be based on features such as stratigraphic persistence, association with other possible reworked elements, and obvious signs of physical reworking (see Birks 1970).

## GENUS ACINOSPORITES Richardson 1965

*Type species*. *Acinosporites acanthomammillatus* Richardson 1965*Acinosporites lindlarensis* Riegel 1968 var. *minor* McGregor and Camfield 1976

Plate 30, figs. 2, 5

*Dimensions* (one specimen). Maximum equatorial diameter 48  $\mu\text{m}$ .*Lithostratigraphical range*. Observatory Group (2c); sample Fair 37.*Remarks*. The Fair Isle miospore closely resembles specimens described by McGregor and Camfield (1976) from sediments of Emsian to Givetian age from the Moose River Basin, Ontario. Although this species has a *Geminospora* organization, the authors follow McGregor and Camfield (1976), by placing it in *Acinosporites*.

## INFRATURMA CRASSITI Bharadwaj and Venkatachala 1962

## GENUS ANEUROSPORA (StreeI) StreeI 1967

*Type species*. *Aneurospora goensis* Steel 1964*Aneurospora greggsii* (McGregor) StreeI in Becker *et al.* 1974

Plate 31, fig. 1

Synonymy, see StreeI in Becker *et al.* (1974, p. 24).*Dimensions* (eight specimens). Maximum equatorial diameter 68–116  $\mu\text{m}$  (mean 84  $\mu\text{m}$ )*Lithostratigraphic range*. restricted to the Bu Ness Group (4a); samples Fair 24, 28, 31, and 33.*Comparisons*. Similar problems to those noted by Lele and StreeI (1969) and StreeI (1972) were encountered in separating this genus from *Geminospora*. A possible synonymy is with *Archaeozonotrilites nalivkini* Naumova as figured by Chibrikova (1977, pl. XIX, fig. 11), but since no description was given, it is impossible to make a detailed comparison. Certain specimens also show similarities with *Geminospora svalbardiae* Allen 1965.

## INFRATURMA CINGULICAVATI Smith and Butterworth 1967

## GENUS CAMPTOZONOTRILETES Staplin 1960

*Type species*. *Camptozonotrilites vermiculatus* Staplin 1960

*Camptonotriletes aliquantus* Allen 1965

Plate 30, figs. 3, 4

*Dimensions* (one specimen). Maximum exoexine diameter 77  $\mu\text{m}$ , maximum intexine diameter 57  $\mu\text{m}$ .

*Lithostratigraphic range*. Ward Hill Group (1b), sample Fair 66.

*Remarks*. The known stratigraphic occurrences for this species are Siegenian to Lower Eifelian (Allen 1967); Upper Siegenian to Lower Emsian (Massa and Moreau-Benoit 1976), and lower Eifelian (Riegel, 1973, 1974). These occurrences are significantly different from the Givetian age assigned to the Fair Isle succession, and its appearance may be the result of reworking.

Genus *DENOSPORITES* Berry emend., Potonié and Kremp 1954

*Type species*. *Densosporites covensis* Berry 1937

*Remarks*. Butterworth *et coll.* 1964 (and in Staplin and Jansonius 1964) in an emendation of the densospora group of miospores, provided unified limits (based largely on Carboniferous material) for the subdivision of generic groups. These genera have not proved applicable for the Devonian densosporites from Fair Isle, but until a more unified revision is carried out, we feel they should be retained.

*Densosporites devonicus* Richardson 1960

Plate 31, fig. 12

*Dimensions* (thirty-six specimens). Maximum equatorial diameter 55–120  $\mu\text{m}$  (mean 85  $\mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Group (1b to 4a). In all samples examined.

*Remarks*. Richardson (1965), in his study of Middle Devonian miospores from the Orcadian Basin, gave the sculptural details, and the relative widths of the light and dark zones of the cingulum as criteria for distinguishing *Densosporites devonicus* from *D. orcadensis*. These same criteria were used in Fair Isle in an attempt to substantiate the differences between the two species, but no systematic variation of these characters, as claimed by Richardson (1965, p. 581), was found. McGregor and Camfield (1976) and McGregor (1979*b*) also had difficulty in distinguishing between the two species. This raises doubts as to the significance of the stratigraphic distribution of the two species as recorded by Richardson (1965).

Genus *SAMARISPORITES* Richardson 1965

*Type species*. *Samarisporites orcadensis* (Richardson) Richardson 1965.

## EXPLANATION OF PLATE 31

All figures  $\times 400$  unless otherwise stated.

Fig. 1. *Aneurospora greggsii* (McGregor) Streef 1974. Fair 31.8, 28.5, 100.6

Fig. 2. *Cirratriradites avius* Allen 1965. Fair 66.2, 12.8, 95.2

Fig. 3. *Samarisporites orcadensis* (Richardson) Richardson 1965. Fair 31.5, 12.1, 104.5

Figs. 4, 7. *Cirratriradites* sp. A. 4,  $\times 1000$ . Detail of distal sculpture. 7,  $\times 400$ . Fair 66.9, 13.9, 110.6

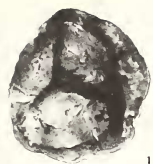
Figs. 5, 6. *Samarisporites mediconus* (Richardson) Richardson 1965. 5, Proximal view. 6, Distal view. Fair 37.71, 13.5, 101.2

Figs. 8, 9. *Samarisporites conannulatus* (Richardson) Richardson 1965. 8, Distal view. 9, Proximal view. Fair 37.80, 5.1, 100.3

Fig. 10. *Auroraspora macromanifestus* (Hacquebard) Richardson 1960. Fair 37.82, 14.8, 112.4

Fig. 11. *Auroraspora micromanifestus* (Hacquebard) Richardson 1960. Fair 37.82, 7.1, 111.0

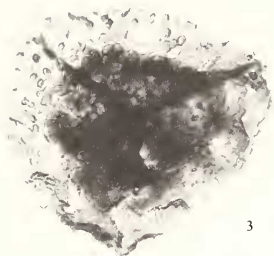
Fig. 12. *Densosporites devonicus* Richardson 1960. Fair 66.3, 4.0, 95.7



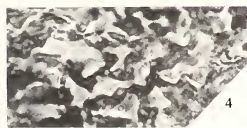
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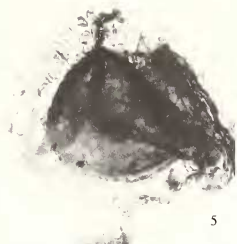
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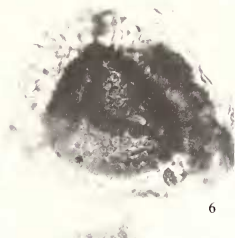
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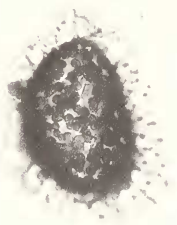
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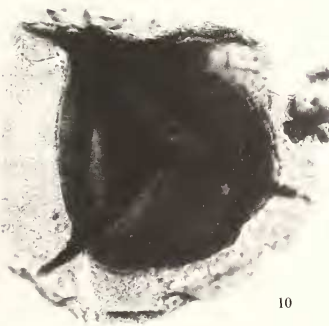
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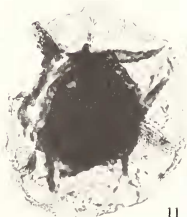
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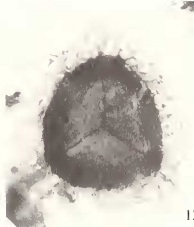
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10



11



12



*Remarks.* The generic status of *Samarisporites* is similar to that of the Devonian *Densosporites*, in being an element of the densospore complex. The genus *Samarisporites*, as originally proposed by Richardson (1965), was to accommodate zonate spores with a variety of solely distal sculptural elements. The justification for the erection of this genus was that its initial assignation to *Cristatisporites* (Potonié and Kremp 1954) was invalid, because the latter has both proximal and distal sculpture. However, it was suggested by Playford (1971), that with the emendation of *Cristatisporites* (Butterworth *et coll.* 1964) as part of a general reorganization of the densospore group, that the use of *Samarisporites* as a distinct generic category could be abandoned. The emendation, however, still includes the possible presence of a proximal sculpture in the form of a ring of setae. It also restricts the distal sculpture to being dominantly mammoid in type, and showing no differentiation in form. The present usage of *Samarisporites* includes forms with a wide variety of distal sculpture (e.g. conical, cristae, verrucae) which cannot be accommodated within *Cristatisporites* (*sensu* Butterworth *et coll.* 1964). It is proposed therefore to use *Samarisporites* for these species, until a more unified set of limits for the densospore group is proposed, which accommodates both Devonian and Carboniferous representatives.

Richardson (1960, 1965) erected three species of *Samarisporites* based largely on sculptural differences and their distribution on the distal surface (e.g. central packing in *S. mediconus*, ring development in *S. conannulatus*). The Fair Isle populations contain intermediate forms, and there is a complete morphological transition series between Richardson's *S. mediconus*, *S. orcadensis*, and *S. conannulatus*, which can be considered as occupying distinct positions on the various trends. It would be interesting to speculate whether the continuous variation this plexus of species exhibits, could be treated in the same way as in the morphon concept recently outlined by Van der Zwan (1979, 1980). However, not enough individuals have yet been found to systematically describe the variation both in a morphological and stratigraphical sense, either to record separate species or varieties in a morphon, or to combine them as a single species.

*Samarisporites mediconus* (Richardson) Richardson 1965

Plate 31, figs. 5, 6

*Dimensions* (eight specimens). Maximum equatorial diameter 73–130  $\mu\text{m}$  (mean 108  $\mu\text{m}$ ), cingulum 10–26  $\mu\text{m}$  wide (mean 17  $\mu\text{m}$ ).

*Lithostratigraphic range.* Ward Hill to Bu Ness Group (1b to 4a); samples Fair 31, 37, and 66.

*Remarks.* Closely resembles the type species, except that there is a greater variety of labra morphology.

*Samarisporites orcadensis* (Richardson) Richardson 1965

Plate 31, fig. 3

*Dimensions* (three specimens). Maximum equatorial diameter 88, 97, and 146  $\mu\text{m}$ . Cingulum width 15–20  $\mu\text{m}$ .

*Lithostratigraphic range.* Observatory and Bu Ness Groups (2c and 4a); samples Fair 31, 33, and 36.

*Remarks.* The three individuals found compare closely with Richardson's holotype. However, they show greater variety of labra morphology in both length and height.

*Samarisporites conannulatus* (Richardson) Richardson 1965

Plate 31, figs. 8, 9

*Dimensions* (five specimens). Maximum equatorial diameter 104–120  $\mu\text{m}$  (mean 113  $\mu\text{m}$ ). Cingulum 14–21  $\mu\text{m}$  wide, maximum width interradially.

*Lithostratigraphic range.* Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 31, 36, 37, and 64.



*Remarks.* Compares closely with the type species except that the labra show a greater amount of variation in length and height.

Genus *CIRRATRIRADITES* Wilson and Coe 1940.

*Type species.* *Cirratriradites saturnii* (Ibrahim) Schopf, Wilson, and Bentall 1944

*Cirratriradites avius* Allen 1965

Plate 31, fig. 2

*Dimensions.* Maximum equatorial diameter 80–130  $\mu\text{m}$  (mean 105  $\mu\text{m}$ ), twenty-eight species measured. Maximum intexine diameter 58–78  $\mu\text{m}$  (mean 67  $\mu\text{m}$ ), eight specimens measured.

*Lithostratigraphic range.* Bu Ness and Ward Hill Groups (4a and 1b); samples Fair 24, 28, 33, 64, and 66.

*Remarks.* Although the type species of this genus is characterized by having distinctive fovea, the formal designation of the genus considered this feature to be of little importance. The assignment by Allen (1965) of *Cirratriradites avius* to this genus, was made on the presence of the reduced sculpture and apparently thin equatorial flange. As it may seem desirable to restrict the use of *Cirratriradites* to miospores with distinctive fovea, it may in the future be necessary to refer this, and other species of similar organization, to a new genus within the densospore complex. The intexine is only seen in overmacerated specimens. *Hymenozonotriletes punctomonogrammos* Arkhangelskaya (in Filimonova and Arkhangelskaya 1963), from the Mosolovian of the Central Devonian Field is clearly similar.

*Cirratriradites* sp. A

Plate 31, figs. 4, 7

*Description.* Miospores trilete; camerate; amb triangular. Suturae indistinct. Exine two-layered, intexine thin and closely appressed to the exoexine. Exoexine infrapunctuate, distally sculptured with muri (2–6  $\mu\text{m}$  high) fused into a cristoreticulate pattern, more dense in central area. Cingulum with an apparent thin margin, but possessing a thicker inner zone.

*Dimensions* (two specimens). Maximum equatorial diameter 125 and 135  $\mu\text{m}$ .

*Lithostratigraphic range.* Ward Hill Sandstone (1b); sample Fair 66 only.

*Remarks.* Differs from *Cirratriradites avius* in having a dense distal sculpture of muri. *Hymenozonotriletes monogrammos* Arkhangelskaya (1963) recorded from the Vorobyevskian, Starskoolian, Chernoyarian, and Mosolovian beds (Eifelian to Givetian) of the Russian Platform, Volga-Urals, and Karatau (Filimonova and Arkhangelskaya 1963, Arkhangelskaya 1974, Raskatova 1969, Chibrikova 1977) is very similar, having a distal network of muri and may prove to be synonymous.

Infraturma *PATINATI* Butterworth and Williams emend. Smith and Butterworth 1967

Genus *CHELINOSPORA* Allen 1965

*Type species.* *Chelinospora concinna* Allen 1965

*Chelinospora concinna* Allen 1965

Plate 30, fig. 9

*Dimensions* (eight specimens). Maximum equatorial diameter 36–65  $\mu\text{m}$  (mean 45  $\mu\text{m}$ ).

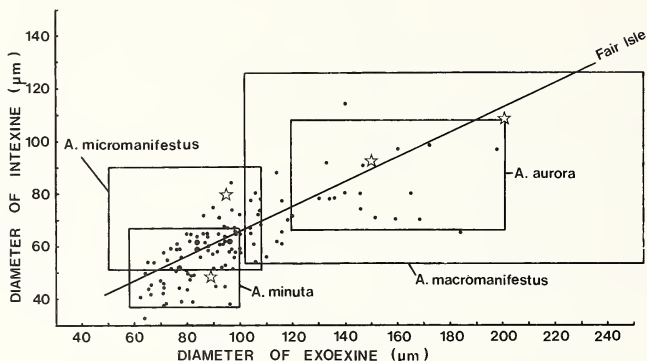
*Lithostratigraphic range.* Observatory Group (3c); samples Fair 36 ad 37.

Infraturma *MONOPSEUDOSACCITI* Smith and Butterworth 1967

Genus *AURORASPORA* Hoffmeister, Staplin, and Malloy 1955

*Type species.* *Auroraspora solisortus* Hoffmeister, Staplin, and Malloy 1955.

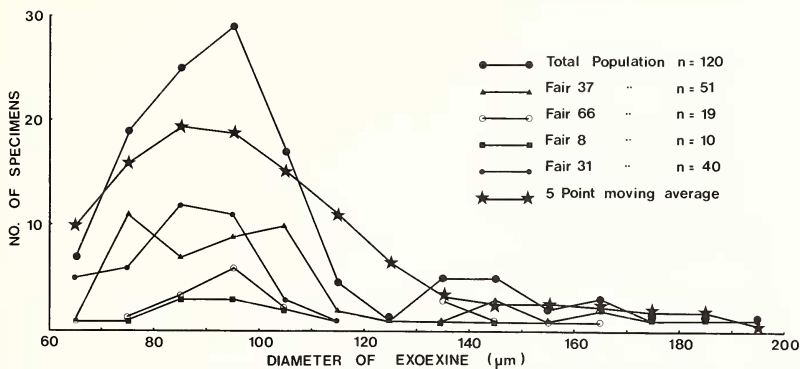
*Population variation in Auroraspora.* Four species of *Auroraspora* have been described from the Middle Devonian of the Orcadian Basin, separated on features such as size, shape, and the relative dimensions of the intexine and exoexine layers. The exoexine and intexine diameters for the type-species populations of *Auroraspora micromanifestus* Richardson 1960, *A. macromanifestus* Richardson 1960, *A. minuta* Richardson 1965, and *A. aurora* Richardson 1960 (with holotype positions



TEXT-FIG. 3. Graphical plot of exoexine and intexine diameters for *Auroraspora* spp. from Fair Isle. The stars mark the holotype positions of species recorded by Richardson 1960, 1965. The regression line is for all *Auroraspora* from Fair Isle.

marked), are plotted in text-fig. 3, and as can be readily seen, the degree of separation is not sufficient to delimit the species purely by this method. The differences could be related to ontogenetic variation in a sporangium, with a changing ratio of exoexine to intexine diameters as the meiospores increase in size. Other characters cited as important in delimiting species, such as shape and eccentricity, are probably not mutually exclusive, and can be related to the presence or absence of labra and their degree of development, which are again themselves a poor classificatory character. Prominent labra on a small meiospore will give a triangular shape, whereas small labra on a large meiospore often results in a circular shape which, when compressed, can increase the eccentricity of the two exine layers. A histogram of the exoexine size distribution (text-fig. 4) also provides valuable information, as a skewed population is seen, which is reminiscent of the pattern produced during the development of heterospory (see Chaloner 1967). Size distribution is also given for individual collection samples, and this shows the effects of some sedimentary sorting. However, bimodal populations are apparent in three of the four assemblages, as well as in the five point moving average line.

It is believed that the species differences are ontogenetic and perhaps reinforced by an incipient heterospory, but more information is needed on meiospore populations found both dispersed and *in situ* from single sporangia, before combining certain meiospore species. A note of caution is also necessary in case the lumping of species causes the loss of potentially valuable morphological data which may be of stratigraphic value as populations of *Auroraspora* succeed each other, with slightly different degrees of size distribution (viz. the possible biostratigraphic value of changing over-all diameters in *Retusotriletes* from the Russian Platform as shown by Naumova 1953, p. 18, text-fig. 6). A sensible course in handling species such as those of *Auroraspora*, is to give precise descriptions and details of dimensions as illustrated in text-figs. 3 and 4.



TEXT-FIG. 4. Frequency distribution plot for *Auroraspora*. Note skewed distribution present in different samples and remains on five point moving average lines.

*Auroraspora macromanifestus* (Hacquebard) Richardson 1960

Plate 31, fig. 10

*Dimensions* (seventeen specimens). Maximum exoexine diameters 120–200  $\mu\text{m}$  (mean 153  $\mu\text{m}$ ), maximum intexine diameters 60–115  $\mu\text{m}$  (mean 83  $\mu\text{m}$ ). See text-fig. 3 for size distributions and ratios of central-body diameter to whole-body diameter (mean 1:4).

*Lithostratigraphic range*. Ward Hill Group to Bu Ness Group (1b to 4a); samples Fair 8, 31, 37, and 66.

*Remarks*. Differs from specimens described by Richardson (1960) from the Middle Devonian of the Cromarty area (Scotland) only in size range.

*Auroraspora micromanifestus* (Hacquebard) Richardson 1960

Plate 31, fig. 11

*Dimensions* (one hundred and two specimens). Maximum exoexine diameter 65–120  $\mu\text{m}$  (mean 89  $\mu\text{m}$ ), maximum intexine diameter 35–85  $\mu\text{m}$  (mean 56  $\mu\text{m}$ ). See text-fig. 3 for size distribution and ratio of central-body diameter to whole-body diameter (mean 1:2).

*Lithostratigraphic range*. Ward Hill to Bu Ness Group (1b to 4a); samples Fair 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

Genus GRANDISPORA (Hoffmeister, Staplin, and Malloy) Neves and Owens 1966 *sensu* Playford 1971

*Type species*. *Grandispora spinosa* Hoffmeister, Staplin, and Malloy 1955.

*Grandispora ?naumovii* (Kedo) McGregor 1973

Plate 32, fig. 5

*Description*. Miospore trilete, camerate, amb ovate. Suturae accompanied by wavy labra up to 6.5  $\mu\text{m}$  in height and individually 2  $\mu\text{m}$  wide. Exine two-layered, intexine laevigate, indistinct, exoexine 1  $\mu\text{m}$  thick, shagreenate, distally sculptured with sparse, gently tapering spines. There are eleven spines around the equatorial periphery which measure up to 20  $\mu\text{m}$  in length.

*Dimensions* (one specimen). Exoexine diameter  $130 \times 106 \mu\text{m}$ , intexine diameter  $80 \times 62 \mu\text{m}$ .

*Lithostratigraphic range*. Observatory Group (2c); sample Fair 37.

*Comparisons*. This miospore closely resembles *Grandispora ?naumovii* described by McGregor and Camfield (1976) from the Middle Devonian of the Hudson Bay area (Canada) and by McGregor (1973) from the Middle Devonian of Gaspé (Canada).

*Grandispora velata* (Eisenack) Playford 1971

Plate 32, fig. 2

Synonymy, see Owens 1971, p. 46

*Dimensions* (nine specimens). Maximum exoexine diameter  $94\text{--}123 \mu\text{m}$  (mean  $111 \mu\text{m}$ ), maximum intexine diameter  $57\text{--}80 \mu\text{m}$  (mean  $70 \mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 36, 37, and 66.

*Comparisons*. The Fair Isle population differs from the type population in having a slightly smaller sculptural size range.

*Grandispora protea* (Naumova) Moreau-Benoit 1980

Plate 32, figs. 3, 4

*Dimensions* (ten specimens). Maximum exoexine diameter  $84\text{--}184 \mu\text{m}$  (mean  $136 \mu\text{m}$ ), maximum intexine diameter  $39\text{--}97 \mu\text{m}$  (mean  $70 \mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 36, 37, and 66.

Genus VELAMISPORITES Bharadwaj and Venkatachala 1962

*Type species*. *Velamisporites rugosus* Bharadwaj and Venkatachala 1962.

*Remarks*. Evans (1970) has interpreted the organization of the genus *Perotrilites* Erdtman ex Couper 1953 as being zonate and not perinate as previously supposed (see Playford 1971). Prior to this, Palaeozoic perinate miospores were placed in *Perotrilites*, but these are now removed to *Velamisporites*, which was originally thought to be a junior synonym, but now forms a satisfactory genus for miospores with such an organization.

*Velamisporites* sp. A

Plate 32, fig. 1

*Description*. Miospores trilete, camerate, amb triangular to rounded. Suturae accompanied by labra commonly  $1.5\text{--}2.5 \mu\text{m}$  high (maximum  $4 \mu\text{m}$ ) which continue as folds on to the perine layer. Exine three-layered; intexine

EXPLANATION OF PLATE 32

All figures  $\times 400$  unless otherwise stated.

Fig. 1. *Velamisporites* sp. A.  $\times 1000$ . Fair 66.2, 19.5, 102.2

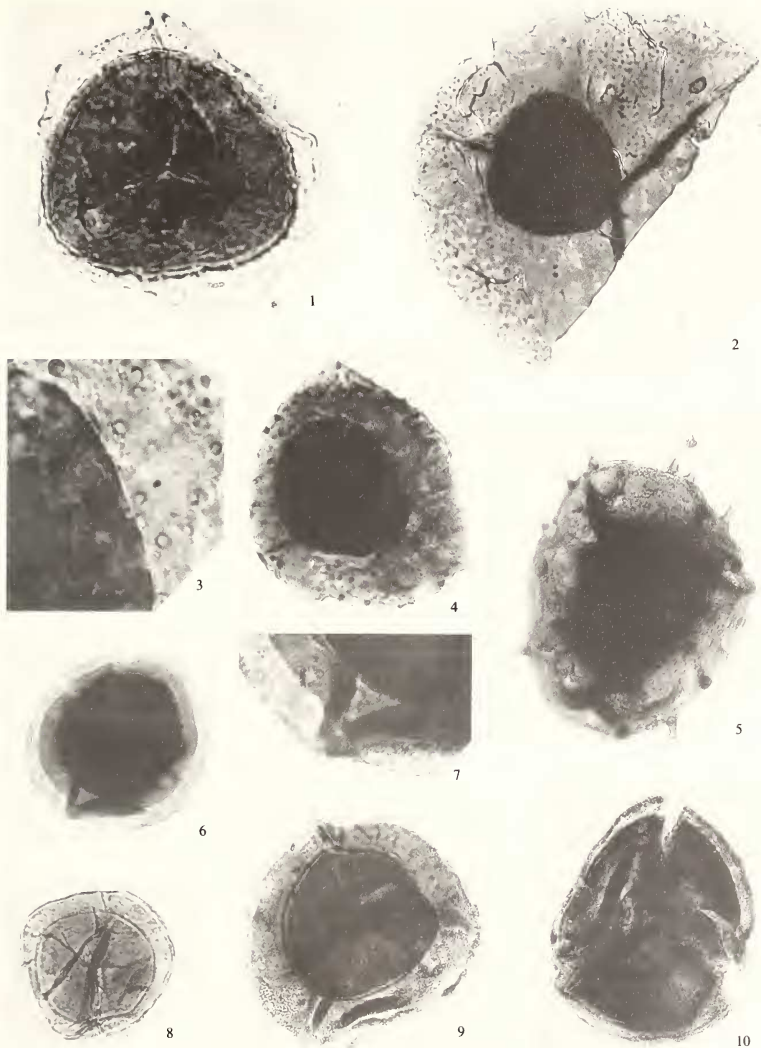
Fig. 2. *Grandispora velata* (Eisenack) Playford 1971. Fair 37.64, 14.3, 100.7

Figs. 3, 4. *Grandispora protea* (Naumova) Moreau-Benoit 1980. 3, detail of distal sculpture  $\times 1000$ . 4,  $\times 400$ . Fair 37.71, 49.5, 108.1

Fig. 5. *Grandispora ?naumovii* (Kedo) McGregor 1973. Fair 37.80, 12.5, 93.2

Figs. 6, 7. *Rhabdosporites* sp. A. 6,  $\times 400$ . 7,  $\times 1000$ : detail showing three wall layers. Fair 37.71, 44.4, 95.1

Figs. 8-10. *Rhabdosporites langii* (Eisenack) comb. nov. 8, 'parvulus' type Fair 37.62, 19.4, 94.60. 9, 'langii' type Fair 37.80, 40.2, 105.5. 10, 'parvulus' type, compare with *Geminispora*. Fair 37.82, 40.2, 105.5



MARSHALL and ALLEN, Devonian miospores

laevigate, often indistinct, closely appressed to the exoexine. Exoexine commonly infrapunctate, 1.5–4  $\mu\text{m}$  thick, with an interradial maximum. Perine wrinkled (especially on the contact areas, where it forms muroid folds) 0.25–0.5  $\mu\text{m}$  thick, sparsely sculptured with parallel sided, flat-topped rods (up to 1  $\mu\text{m}$  high) mixed with grana and coni (up to 0.5  $\mu\text{m}$  high).

*Dimensions* (seven specimens). Maximum perine diameter 61–76  $\mu\text{m}$  (mean 66  $\mu\text{m}$ ), maximum exoexine diameter 46–67  $\mu\text{m}$  (mean 55  $\mu\text{m}$ ). Separation between these two layers 5–17  $\mu\text{m}$  (mean 11  $\mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Groups (1b to 4a); samples 31, 37, and 66.

*Remarks*. Many of the described species of Devonian *Perotrilites* resemble the Fair Isle material. However, all differ in size and minor sculptural details. *Perotrilites pannosus* Allen 1965 has a thick perine with more folds, and coni with bifurcating tips. *P. conatus* Richardson 1965 has a denser sculpture of cones and a different ratio of wall-layer dimensions. *P. aculeatus* Owens 1971 has a thinner perine and a sculpture of cones. *P. selectus* (Arkhangelskaya) McGregor and Camfield 1976 is larger and has cones.

#### GENUS RHABDOSPORITES Richardson emend.

*Type species*. *Rhabdosporites langii* (Eisenack) Richardson 1960.

*Emended diagnosis*. Miospores radial, trilete, amb circular to triangular. Camerate, with separate exoexine and intexine attached at the proximal pole. Exoexine with or without limbus, sculptured with low rods, coni, and grana. Intexine laevigate.

*Discussion*. In 1960 the genus *Rhabdosporites* was erected to accommodate certain distinctive pseudosaccate miospores previously described by Eisenack (1944), Lang (1925), and others. Its main distinguishing features according to Richardson (1960) were the proximally attached non-limbate bladder and the evenly distributed over-all sculpture of closely packed rods with parallel sides and flat tops. Subsequently, the genus, and particularly the type species *Rhabdosporites langii*, has proved to be one of the most common Devonian miospores, showing a wide stratigraphic range and geographic distribution. Later workers, however, have not kept to the original diagnosis, placing in *Rhabdosporites* limbate miospores as well as those with sculptural elements containing grana and coni. There have been some good arguments for this; Owens (1971) pointed out a discernible limbus in the illustration of the type species, and Lele and Streele (1969, p. 102) commented on some well-preserved specimens from the same horizons as Richardson's material, with coni often as a dominant element, as well as rods with truncated tips. It would seem sensible therefore to widen the scope of the genus to include similar spores, with both a limbus and a more variable ornament of reduced size. Camerate spores with coarser sculpture are included in other genera (e.g. *Grandispora*). In widening the generic concept of *Rhabdosporites*, we are aware of the close similarity between small specimens of *Rhabdosporites* and *Geminispora* (Balme) Owens 1971, which has been mentioned by previous authors (e.g. Lele and Streele 1969, p. 103). *Geminispora* is typified by a thin-walled intexine either closely appressed to, or showing a variable degree of separation from, a sculptured exoexine with a thickened distal surface. This organization is difficult to distinguish (without recourse to microtome sections) from a limbate pseudosaccate miospore (see Pl. 32, fig. 8) with a high intexine–exoexine cavity ratio as seen in small *Rhabdosporites*. Various indirect criteria were used in attempts to distinguish the forms, based on the presence of the thickened distal surface which is a characteristic of the *Geminispora* group. It might be expected that this would hold the miospore rigid, with the intexine and proximal exoexine positioned in the shaped distal exoexine 'cup', thus limiting the eccentricity between the two bodies when compressed. The thickened distal exoexine would also deflect and restrict exoexine folding, to give different folding characteristics on the proximal and distal surfaces. Further evidence for the similarity (or inability to easily distinguish) between *Rhabdosporites* and *Geminispora* comes from the study of *in situ* spores (see Allen 1980), where spores assignable to *Rhabdosporites* and *Geminispora* are recorded from closely related progymnosperms.

*Rhabdosporites langii* (Eisenack) comb. nov.

Plate 32, figs. 8–10

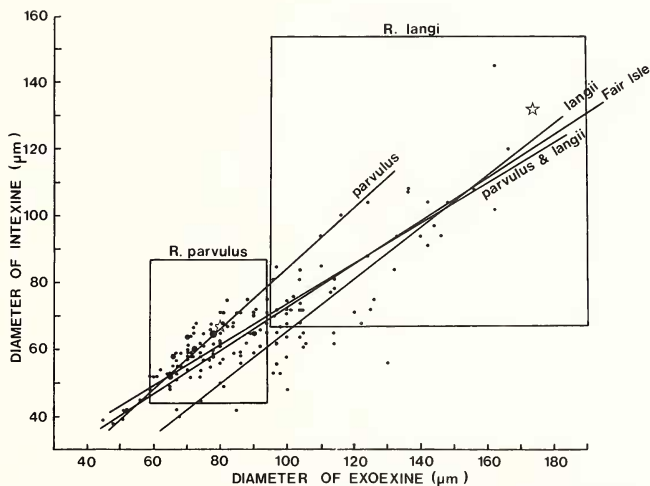
- 1925 Type B Lang, p. 256, pl. 1, figs. 3–6.  
 1944 *Triletes langii* Eisenack, p. 112, pl. 12, fig. 4.  
 1960 *Rhabdosporites langii* (Eisenack) Richardson, p. 54, pl. 14, figs. 8, 9.  
 1963 *Rhabdosporites firmus* Guennel, p. 256, fig. 12.  
 1965 *Rhabdosporites parvulus* Richardson, p. 588, pl. 93, figs. 5–7.  
 1971 *Rhabdosporites micropaxillus* Owens, p. 49, pl. 15, figs. 3–7.  
 1973 *Rhabdosporites* sp. Hamid, p. 202, pl. 10, no. 1.

For additional synonymies, see Moreau-Benoit, 1980, pp. 29 and 30.

*Dimensions* (one hundred and sixty-five specimens). Maximum exoexine diameter 45–166  $\mu\text{m}$  (mean 90  $\mu\text{m}$ ), maximum intexine diameter 39–146  $\mu\text{m}$  (mean 65  $\mu\text{m}$ ).

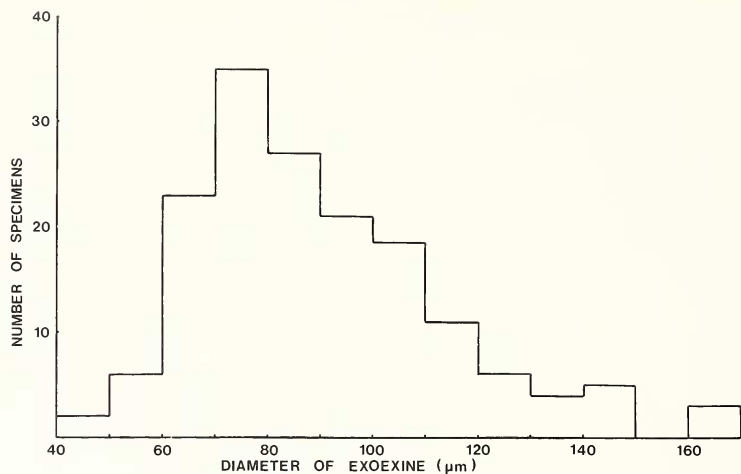
*Lithostratigraphic range*. Ward Hill to Bu Ness Group (1b to 4a)—samples Fair 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

*Remarks*. *Rhabdosporites parvulus* Richardson 1965 was associated with *R. langii* in all the samples studied, and attempts were made to discriminate between the two species as did Richardson (1965, p. 588), using a graphical plot of exoexine and intexine diameters. A graph of the data from Fair Isle (text-fig. 5) shows no obvious separation into two populations, but a gradual change in the ratio of



TEXT-FIG. 5. Size variation in *Rhabdosporites langii* from Fair Isle compared with published data from the Orcadian Basin. Reduced major axis lines are seen to be closely comparable between Fair Isle and a combined *R. langii* and *R. parvulus* population from the Orcadian Basin. Separate R.M.A. lines for *R. langii* Richardson 1960 and *R. parvulus* Richardson 1965 only apply to parts of the population which is clearly seen to be continuous. The boxes show the limits of the type-species population, and the stars show the holotype position. Larger points refer to two or three individuals.





TEXT-FIG. 6. Frequency plots for *Rhabdosporites* exoexine diameters.

the exoexine and intexine diameters as the spore size increases. Further, the data from Richardson's graph were replotted as a single population, and reduced major axis lines calculated for the combined data. It can be seen from this result that there is no obvious difference between regression lines for combined populations of *R. langii* and *R. parvulus* and similar lines calculated for the separate species as defined by Richardson. A regression line calculated for the Fair Isle population shows a strong similarity to the combined Richardson plot. A frequency distribution plot of the exoexine diameters (see text-fig. 6) gives a smooth population curve and no sign of bimodality, which might be expected if two distinct species were present. The stratigraphic range chart of Richardson (1965, opposite p. 590) shows a disjunct appearance for *R. parvulus* only in the Eday Group, whilst the text (p. 588) does indicate its appearance further down the sequence, such that it is coincident with *R. langii*. *Rhabdosporites* has also been identified as an *in situ* miospore in both *Tetraxylopteris schmidtii* (Beck) Bonamo and Banks 1967 and in *Rellimia thompsonii* Leclercq and Bonamo 1973 (in Leclercq and Bonamo 1971). These occurrences also provide further information on the similarity between *Rhabdosporites langii* and *R. parvulus*, as both of these descriptions also comment on the presence of miospores with a size range including both *R. langii* and *R. parvulus* in the same sporangium. These authors also consider that the differences described by Richardson are ontogenetic, and as miospores matured inside a sporangium, the exoexine expanded more rapidly than the intexine, showing an increasing ratio between the two wall diameters as well as increased sculpture size. It is suggested that the continua seen in the dispersed species can be attributed to this ontogenetic variation, and that with the size distribution data collected for these *in situ* miospores to confirm this similarity there is now no reason to consider *langii* and *parvulus* as separate species. If the enlarged concept of the genus to include limbate spores with sculptural elements of grana and conii as well as rods is accepted, then *R. micropaxillus* Owens 1971 is intermediate between *R. langii* and *R. parvulus* and can be regarded as synonymous; as are *R. firmus* Guenel 1963 and *Rhabdosporites* sp. Hamid 1973, which similarly differ only in the presence of grana and conii amongst the sculptural elements.



*Rhabdosporites* sp. A

Plate 32, figs. 6, 7

*Description.* Miospores trilete; amb circular; exine three-layered. Suturae length equal to inner body radius, accompanied by simple labra (each 1  $\mu\text{m}$  wide). The two inner wall layers laevigate, homogeneous; the outer wall infrapunctate, sculptured with conic, rounded-tipped rods, and grana (0.25–1  $\mu\text{m}$  high). The three walls are variable in thickness and carry folds which show them to be separated except on the proximal surface. Outer wall appears limbate.

*Dimensions* (three specimens). Maximum diameters: outer wall 90  $\mu\text{m}$ , 101  $\mu\text{m}$ , 96  $\mu\text{m}$ ; middle wall 74  $\mu\text{m}$ , 67  $\mu\text{m}$ , 80  $\mu\text{m}$ ; inner wall 58  $\mu\text{m}$ , 43  $\mu\text{m}$ , 61  $\mu\text{m}$ . Optically discernible wall thicknesses: outer wall 2.0  $\mu\text{m}$ , 2.5  $\mu\text{m}$ , 0.5  $\mu\text{m}$ ; middle wall 0.25  $\mu\text{m}$ , 1.0  $\mu\text{m}$ , 0.5  $\mu\text{m}$ ; inner wall 2.0  $\mu\text{m}$ , 1.5  $\mu\text{m}$ , 2.0  $\mu\text{m}$ .

*Lithostratigraphic range.* Observatory Group (2c); sample Fair 37.

*Remarks.* *Rhabdosporites* sp. A of Richardson 1965 is similar in having three layers, and differs only on size and minor sculptural features. ?*Calyptosporites* sp. A Mortimer and Chaloner 1972 appears to be conspecific, and these authors also suggest a possible further synonymy with a miospore figured by Ozolin'a (1960a, pl. 1, fig. 29) and identified as *Archaeozonotriletes micromanifestus* var. *minor* Naumova. Hemer and Nygreen (1967) illustrate a trivalved miospore as *Rhabdosporites* sp. but as no description was provided, further comparison is impossible. Massa and Moreau-Benoit (1976) record the presence of *Rhabdosporites* sp. A Richardson, from their palynozones 6 and 7, which are dated as late Givetian and early Frasnian.

Similar *in situ* miospores have been recovered by *Tetraxylopteris schmidtii* Bonamo and Banks 1967, where they occurred in subordinate numbers to specimens similar to *Rhabdosporites langii* and *R. parvulus*. Bonamo and Banks (1967) included a personal communication from Richardson, which expressed the opinion that the extra layer could have arisen by a splitting of one of the two wall layers of *Rhabdosporites*. The middle wall of the Fair Isle specimens appears to be a more definite layer than in similar miospores illustrated from *T. schmidtii*. A possible explanation for this difference is that the third layer may be a teratological feature, and a possible way of showing this, as opposed to the wall splitting hypothesis, is to sum the various thicknesses of the wall layers. It might be expected that any wall splitting would provide a total equal to the mean intexine plus exoexine value of a normal *Rhabdosporites*. Unfortunately the data are not available to show this, as no wall-thickness measurements are provided for the Cromarty populations of these spores. The presence of a limbate wall feature would also create difficulties and uncertainty in measurement.

## INCERTAE SEDIS

Genus *HYSTRICOSPORITES* McGregor 1960

*Type species.* *Hystricosporites delectabilis* McGregor 1960.

*Hystricosporites* cf. *corystus* Richardson 1960

Plate 33, figs. 7–9

*Description.* Miospore trilete; amb circular to triangular, ovate in lateral compression. Suturae accompanied by prominent labra (19–36  $\mu\text{m}$  high, 56–116  $\mu\text{m}$  in length as seen in lateral compression). Exine two-layered, intexine laevigate, closely appressed to the exoexine. Exoexine with paired radial muri on the contact areas (length 20–28  $\mu\text{m}$ , width 4–7  $\mu\text{m}$ ), proximo-equatorially and distally sculptured with 5–14 grapnel-tipped spines (20–52  $\mu\text{m}$  long).

*Dimensions.* Maximum equatorial diameter 60–130  $\mu\text{m}$  (mean 96  $\mu\text{m}$ ), eleven specimens measured. Maximum height (excluding labra) in lateral compression 65–122  $\mu\text{m}$ , six specimens measured.

*Lithostratigraphic range.* Ward Hill to Bu Ness Groups (1b to 4d); samples Fair 8, 24, 31, 33, 36, 37, 64, 66, and 67.

*Remarks.* The Fair Isle population is very similar to *Hystricosporites corystus* Richardson 1962, differing only in gross size. Richardson's *Hystricosporites* cf. *corystus* should not be confused with the Fair Isle miospores.

The proximal radial muri and intexine are seen only in overmacerated specimens. Frequently only the bases of the spines are complete, but when intact the grapnel-tips are of the laterally extended form (see Owens 1971, p. 87). Difficulties were encountered in relating spores with intact spines to those showing proximal lip and intexine detail, because the high maceration levels needed to clear the miospores resulted in severe erosion of the grapnel-tips.

#### Genus ANCYROSPORA Richardson emend. Richardson 1962

*Type species.* *Ancyrospora grandispinosa* Richardson 1960.

#### *Ancyrospora ancyrea* (Eisenack) Richardson 1962

Plate 33, figs. 3, 10

*Dimensions* (seventeen specimens). Maximum equatorial diameter 81–165  $\mu\text{m}$  (mean 120  $\mu\text{m}$ ).

*Lithostratigraphic range.* Ward Hill to Bu Ness Groups (1b to 4a), samples 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

*Remarks.* Placed in *Ancyrospora ancyrea* and not *A. ancyrea* var. *ancyrea* Richardson 1962 because it does not show the wide flange development which characterizes the variety. It conforms to text-fig. 5 (p. 178) of Richardson (1962), and is morphologically average for the three described varieties.

The same maceration problems were encountered in studying this species as with *Hystricosporites* cf. *corystus*, in that it was rare to find completely cleared spores in which the grapnel-tipped spines were preserved.

#### *Ancyrospora ancyrea* cf. var. *brevispinosa* Richardson 1962

Plate 33, figs. 4–6

*Description.* Miospores trilete; amb triangular to subtriangular. Suturæ accompanied by labra (1  $\mu\text{m}$  high). Exine two-layered, intexine laevigate, thin, closely appressed to the exoexine. Exoexine shagreenate, with a dark halo, or triangular darkening in the proximal polar area, contact areas often with sinuous folds. Proximo-equatorially and distally sculptured with grapnel-tipped spines (1–10  $\mu\text{m}$  long), the tips 1–2  $\mu\text{m}$  across have little discernible detail (Pl. 33, fig. 6). Flange development variable (0–12  $\mu\text{m}$  wide) with some very narrow forms (Pl. 33, fig. 5) and others interradially.

*Dimensions* (one hundred and fifty specimens). Maximum equatorial diameter 39–95  $\mu\text{m}$  (mean 65  $\mu\text{m}$ ).

*Lithostratigraphic range.* Ward Hill to Bu Ness Group (1b to 4a); samples 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

#### EXPLANATION OF PLATE 33

All figures  $\times 400$  unless otherwise stated.

Fig. 1. *Geminospira* sp. B. Fair 31.5, 6.3, 101.1

Fig. 2. *Geminospira* sp. A. Fair 31.5, 36.6, 101.7

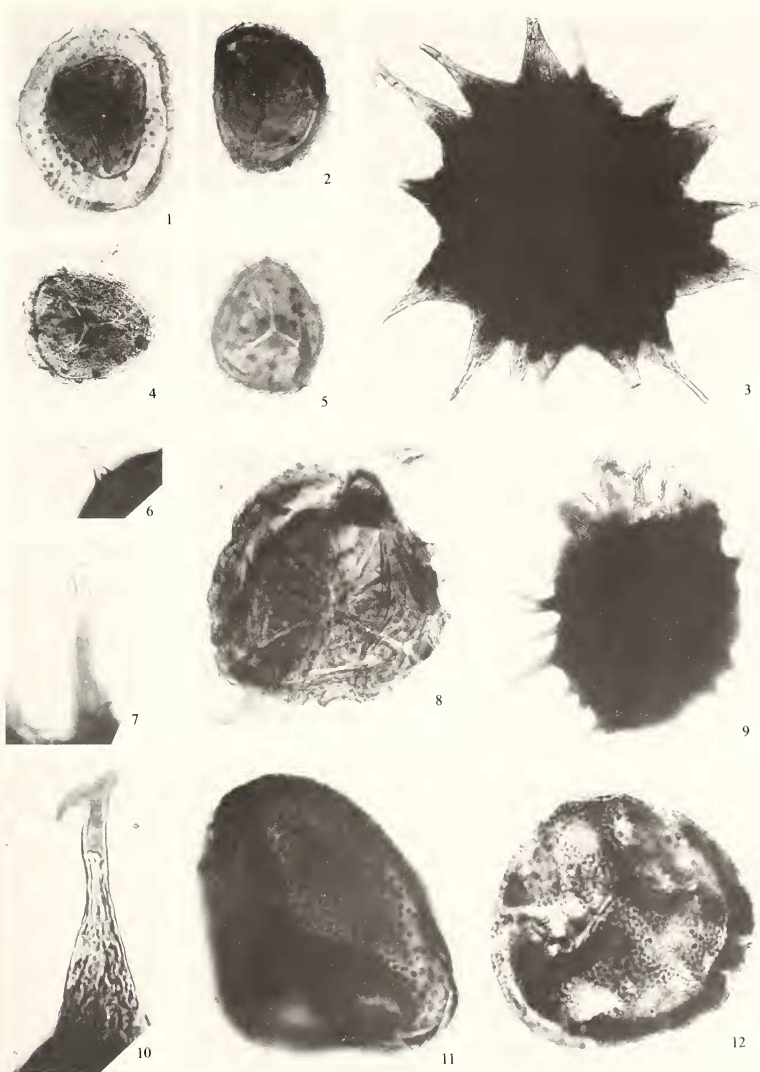
Figs. 3, 10. *Ancyrospora ancyrea* (Eisenack) Richardson 1962. 3, Fair 37.64, 29.3, 107.1. 10, detail of spine process,  $\times 1000$ .

Figs. 4–6. *Ancyrospora ancyrea* cf. var. *brevispinosa* Richardson 1962. 4, wide flange form. Fair 8.1, 11.4, 106.1. 5, narrow flange form. Fair 37.64, 14.4, 96.9. 6, detail of spine process from 5,  $\times 1800$ .

Figs. 7–9. *Hystricosporites* cf. *corystus* Richardson 1960. 7, detail of spine process from 9. 8, well oxidized specimen. Fair 67.30, 100.6, 33.4. 9, dark specimen, lateral compression. Fair 37.63, 9.1, 96.9.

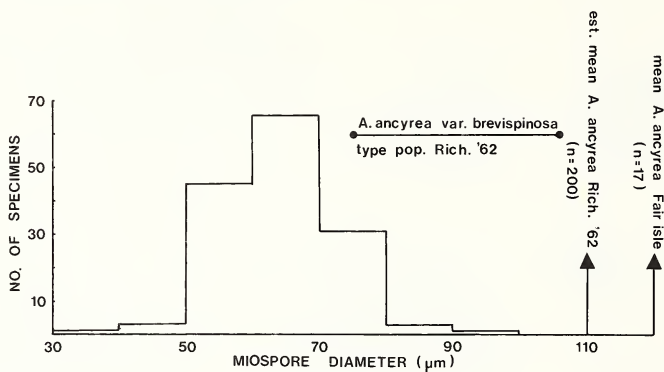
Fig. 11. *Geminospira tuberculata* (Kedo) Allen 1965.  $\times 1000$ . Fair 37.64, 22.4, 99.2

Fig. 12. *Geminospira svalbardiae* (Vigran) Allen 1965.  $\times 1000$ . Fair 28.20, 50.2, 114.3



MARSHALL and ALLEN, Devonian miospores

*Remarks.* This spore is closely similar to *Ancyrospora ancyrea* var. *brevispinosa* Richardson 1962 except in gross diameter, which seems to reflect a genuine difference, as opposed to modifications in the population based in sedimentary sorting processes. The evidence for this (see text-fig. 7) is that whilst the size frequency distributions for *Ancyrospora ancyrea* from both Fair Isle and the Orcadian Basin (see Richardson 1962, p. 185) clearly parallel each other, those for var. *brevispinosa* (this paper) are quite different. It is postulated on a simple model that any sorting process which could modify the size-frequency distributions of the variety *brevispinosa* and cf. *brevispinosa* to this extent, would also show a difference in the *Ancyrospora ancyrea* populations, which is not so.



TEXT-FIG. 7. Frequency plot for *Ancyrospora ancyrea* cf. var. *brevispinosa*. There is a difference in population size range compared with that of Richardson 1962, which is not reflected in *A. ancyrea*.

The much-reduced flange on the exoexine (see Pl. 33, fig. 5) produces some problems in using the genus *Ancyrospora*, which, as defined by Richardson (1962) in his emended diagnosis, has an extended equatorial flange of pseudoflange. The evidence from the Fair Isle sequence suggests that a continua exists from obviously flanged miospores to almost flangeless ones, and therefore in part outside the generic diagnosis. The presence of sinuous surface folds on the exoexine and the occasional appearance of a membranous top exine layer, suggests the possibility that a third layer is developed, similar to *A. fallacia* Urban (1970), and frequently lost on oxidation. Another point of interest is a possible relationship with *Perotrilites bifurcatus* Richardson 1962, which could be interpreted as an overmacrated *Ancyrospora* with the spalling off of a third outer exine layer normally closely appressed to the exoexine.

#### GEMINOSPORA (Balme) Owens 1971

*Type species.* *Geminospira lemurata* Balme 1962

*Discussion.* As well as the difficulties discussed earlier in separating *Rhabdosporites* from *Geminospira*, there is an apparent morphological transition series between *Geminospira* and *Grandispora* in our material. The problem has previously been described in other assemblages by Neves and Owens (1966) and Playford (1971). Where one draws the dividing line between truly camerate miospores such as *Grandispora* which show a clear separation of intexine and exoexine (sensu Playford 1976 and not McGregor 1973), and *Geminospira* which has both widely separated and closely appressed

wall layers in the same population, is at present arbitrary. A further difficulty is that increased separation of wall layers may result from the oxidative processes used in clearing the highly carbonized Fair Isle miospore assemblages.

*Geminospora tuberculata* (Kedo) Allen 1965

Plate 33, fig. 11

*Dimensions* (eleven specimens). Maximum equatorial diameter 42–67  $\mu\text{m}$  (mean 56  $\mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 28, 31, 33, 36, 37, 66, and 67.

*Remarks*. The Fair Isle material differs only from that described by Allen (1965) in having slightly smaller sculptural elements and greater variation of haplotypic features. The emendation of *Archaeozonotriletes tuberculatus* Kedo by Allen (1965) to accommodate the Spitsbergen population of *Geminospora* is open to some modification as more Soviet miospores of closely related species have now been described, into which parts of the population could be accommodated. We believe that there are problems of synonymy between *Geminospora* and *Archaeozonotriletes* (sensu Naumova) and a thorough separate revision is preferable to minor amendments made here.

*Geminospora svalbardiae* (Vigran) Allen 1965

Plate 33, fig. 12

*Dimensions* (nine specimens). Maximum equatorial diameter 47–72  $\mu\text{m}$  (mean 58  $\mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 8, 31, 33, 36, 37, and 66.

*Remarks*. The population described by Allen (1965) is very similar to the Fair Isle material, differing only in being of larger over-all size and having a more reduced sculpture. Possible synonymies include *Geminospora maculata* Taugourdeau-Lantz 1967 and *Geminospora plicata* Clayton and Graham 1974 (nomen illeg.—junior homonym for *G. plicata* Owens 1971). Both these forms, as described, are similar, and differ only in minor features of size and type of sculpture.

*Geminospora* sp. A

Plate 33, fig. 2

*Description*. Miospore trilete; amb circular to triangular. Suturae straight and extending to the intexine margin. Exine two-layered; intexine laevigate, thin with conspicuous folds, and of variable separation from the exoexine. Exoexine 5  $\mu\text{m}$  thick, with a sculpture of coni (2  $\mu\text{m}$  high), some of which are arcuate or bifiform, typical height 2  $\mu\text{m}$ .

*Dimensions* (one specimen). Maximum equatorial diameter 70  $\mu\text{m}$ .

*Lithostratigraphic range*. Observatory Group (2c); sample Fair 37.

*Remarks*. Similar miospores have been described from the Soviet Union as *Archaeozonotriletes visendus* Chibrikova, *A. visendus* var. *echinatus* Chibrikova, *A. egregius* Naumova, *A. tuberculatus* var. *aculeatus* Raskatova, *A. acutus* Raskatova, *A. pensus* Kedo, *A. lasius* var. *minor* Naumova. Unfortunately its single occurrence in the Fair Isle sequence limits its value at present.

*Geminospora* sp. B

Plate 33, fig. 1

*Description*. Miospores trilete; amb roughly triangular. Suturae simple or accompanied by thin labra commonly 1–2  $\mu\text{m}$  high (maximum 5  $\mu\text{m}$ ). Exine two-layered with exoexine and intexine layers separate, attached only at the proximal pole. Intexine laevigate, thin, showing a variation in degree of separation. Exoexine 2.5–14  $\mu\text{m}$  thick (mean 6.5  $\mu\text{m}$ ) with individuals showing an interradial maximum (up to 2.5  $\mu\text{m}$  thicker). Exoexine sculpture

(except for contact areas) with cones and fine tapering spines 1–5  $\mu\text{m}$  long (mean 2.5  $\mu\text{m}$ ), denser and of greater length distally than equatorially or proximo-equatorially.

*Dimensions* (twenty-seven specimens). Maximum exoexine diameter 65–140  $\mu\text{m}$  (mean 89  $\mu\text{m}$ ).

*Lithostratigraphic range*. Ward Hill and Observatory Groups (1b to 2c); samples. Fair 37 and 66.

*Remarks*. *Archaeozonotrites comptus* Naumova (1953), *A. comptus* var. *expletivus* Chibrikova (1959) (see also Raskatova 1969 and Chibrikova 1962, 1977), *A. tuberculatus* Kedo var. *minor* Kedo (1976), and *A. tuberculatus* Kedo var. *triangulatus* Kedo 1976 are all miospores of a similar construction, sculpture, and size. However, their descriptions are not detailed enough to confidently place *Geminospora* sp. B into any one of these species.

#### SEQUENCE AND STRATIGRAPHIC SIGNIFICANCE OF THE MIOSPORE ASSEMBLAGES

The number of miospore-bearing horizons has proved to be small, but fortunately of wide distribution. This is shown for selected miospore taxa in text-fig. 8. There is no major palynostratigraphic change in the succession until the Bu Ness Group, which is characterized by the incoming of *Aneurospora greggsii* and *Convolutispora disparalis*.

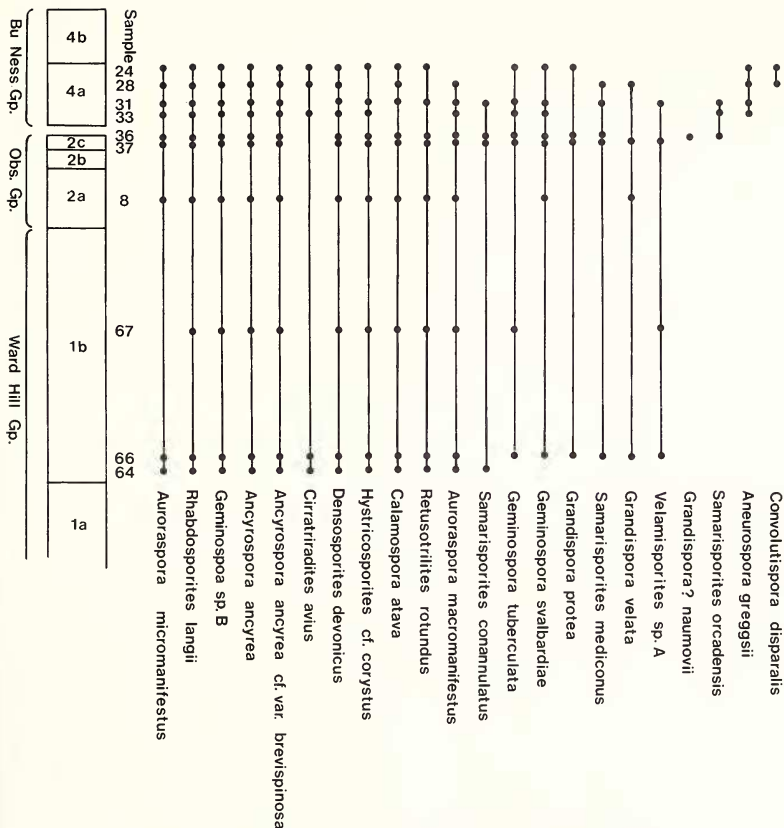
The general problems of Devonian palynostratigraphy have been discussed at length by several authors (Owens and Richardson 1972; Richardson 1974; and McGregor 1979a) so will only be briefly alluded to in this stratigraphical synthesis. The total stratigraphical ranges for some of the taxa from Fair Isle are plotted in text-fig. 9 and show long ranging distributions. This type of compilation suffers from the lack of miospore assemblages securely dated by independent means (notably Ammonoids, Conodonts), which can be compared accurately with the type sections of the traditional stages. The data suggests a Givetian age for the Fair Isle assemblages but does not place reliance on the restricted ranges of several poorly known species. A more precise correlation is possible by drawing comparisons with selected areas containing well-dated assemblages.

#### *Comparisons with European Assemblages (excluding the Soviet Union but including Spitsbergen)*

The spore sequences described by Richardson (1965) for the Orcadian Basin are now geographically the closest described Devonian palynofloras to Fair Isle. The abundance in Fair Isle of *Ancyrospora ancyrea* cf. var. *brevispinosa* with the first appearance of *Grandispora ?naumovii* suggest possible equivalence with the Eday Beds. An interesting comparison, and possibly significant, is the very rare occurrences of *Emphanisporites* spp. in both Fair Isle and the Orcadian Basin, which are not thought to be the result of reworking (Clayton *et al.* 1977). A major difference between the Fair Isle beds and the Eday Group on Orkney is the complete absence of *Geminospora* spp. in the latter, compared with its relative abundance and diversity in Fair Isle. It could be argued that this is of stratigraphic importance, except that *Geminospora* spp. is known from independently dated Givetian beds from over a wide area including Illinois (Sanders 1968), Spitsbergen (Allen 1965), and southern England (Mortimer and Chaloner 1972). It has been suggested (Richardson 1967) that the control is ecological, and this will be discussed later.

The spore assemblages described from borehole material of southern England by Mortimer and Chaloner (1972) compare quite closely, but add little to the specific age assignment apart from confirming it as Givetian. Detailed comparisons of the Fair Isle spore assemblages can also be made with the sequences described by Streeel and associates (reviewed in Streeel 1972) from Belgium and northern France. Streeel in a discussion of marker spores for the Givetian–Frasnian boundary considers the first appearances of *Aneurospora greggsii*, *Ancyrospora langii*, and *Samarisporites hesperus* to be of major significance. The occurrence of *Aneurospora greggsii* in the Bu Ness Group does suggest that this higher part of the Fair Isle sequence is late Givetian in age and close to the Givetian–Frasnian boundary. Streeel (1972) also gave the range of *Grandispora velata* and *?Rhabdosporites langii* (closely comparable with the Fair Isle form) from the Tournai borehole as





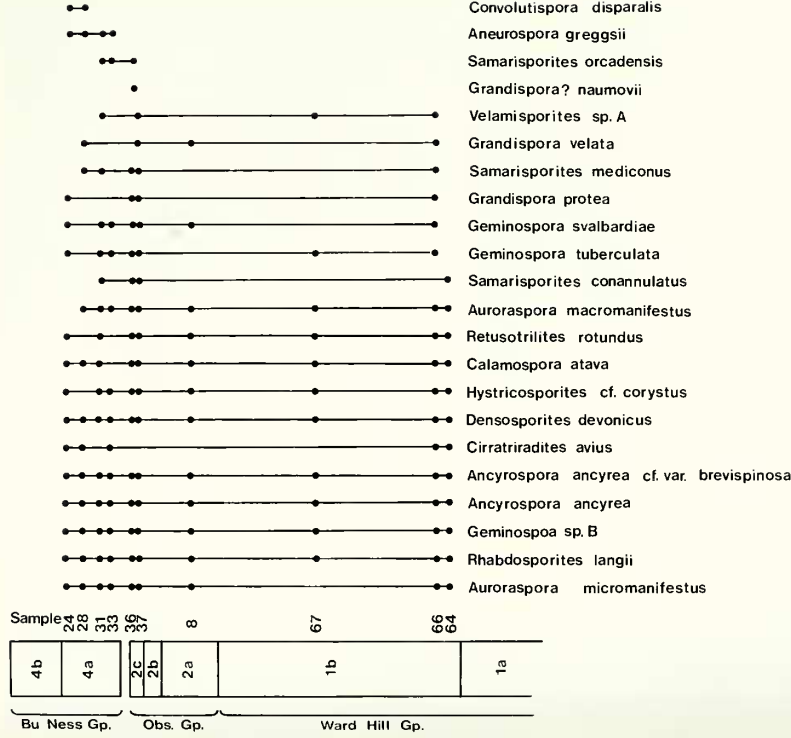
TEXT-FIG. 8. Stratigraphical distribution of selected miospores in Fair Isle.

overlapping the range of *Aneurospora greggsii*, but the information was not sufficient to suggest that this was of any widespread stratigraphic value. Loboziak and Streel (1980), in a study of Givetian and Frasnian rocks from Boulonnais (France), considered several species to be of importance in delimiting beds of late Givetian age, including *Chelinospora concinna*, *Ancyrospora ancyrea* var. *brevispinosa*, and *Convolutispora disparalis*, all found in the Fair Isle section.

In Spitsbergen, Allen (1967) described a zonal scheme of three assemblages for the Devonian rocks. The Fair Isle sequence has many similarities to the *triangulatus* assemblage with *Geminospora tuberculata*, *Cirratiradites avius*, *Convolutispora disparalis*, *Densosporites devonicus*, *Chelinospora concinna*, and *Grandispora protea* in common. The *triangulatus* assemblage was assigned to the







TEXT-FIG. 8. Stratigraphical distribution of selected miospores in Fair Isle.

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'SPORE TAXA	STAGE																						
	<i>Acinosporites lindlarensis</i>	<i>Ancyrospora ancyrea</i>	<i>Aneurospora greggsii</i>	<i>Auroraspora macromanifestus</i>	<i>A. micromanifestus</i>	<i>Calamospora atava</i>	<i>Chelinospora concinna</i>	<i>Cirratiradites avus</i>	<i>Convolutispora disparalis</i>	<i>Densosporites devonicus</i>	<i>Geminosporea svalbardiae</i>	<i>G. tuberculata</i>	<i>Grandispora ? naumovii</i>	<i>G. protea</i>	<i>G. velata</i>	<i>Hystricosporites corystus*</i>	<i>Rhabdosporites sp.A</i>	<i>R. langii</i>	<i>Retusotriolites rotundus</i>	<i>Samarisporites conannulatus</i>	<i>S. mediconus</i>	<i>S. orcadensis</i>	
Famennian		•	•			•					•							•	•				
Frasnian		•	•		•	•	•			•	•	•		•	•	•	•	•	•				
Givetian	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eifelian	•	•		•	•	•	•	•		•	•		•	•	•	•			•	•	•	•	•
Emsian	•	•	•	•		•	•	•			•			•	•	•			•	•		•	
Siegnian															•					•			
Gedinnian																				•			

TEXT-FIG. 9. Stratigraphical distribution of selected taxa which occur on Fair Isle. \* Refers to comparison record.

Givetian by Allen (1967) although the lower part is without *Densosporites devonicus* and is considered to be of possible Eifelian age (McGregor and Camfield 1976).

A detailed study has been made by Beju (1972) on rocks of Devonian age from the Moesian platform of Romania. The Eifelian subzone (D2a) has the long-ranging *Grandispora protea* and *Calamospora atava* in common with Fair Isle. The Givetian subzone (D2b) is more similar, with *Ancyrospora ancyrea*, *Rhabdosporites langii*, *Grandispora velata*, *Auroraspora macromanifestus*, and *Densosporites devonicus* in common. These last three are considered by Beju to be specifically characteristic of this subzone. The Frasnian zone (D3) contains *Geminosporea svalbardiae*, *G. tuberculata*, *Rhabdosporites parvulus*, and *Auroraspora micromanifestus*.

#### Comparisons with North American Assemblages

The Frasnian Ghost River spore assemblage described from Alberta by McGregor (1964) compares with the Bu Ness Group of the Fair Isle sequence only in the presence of *Aneurospora greggsii*. McGregor (in McGregor and Uyeno 1972) described a sequence of spore assemblages from the Canadian Arctic Archipelago, and of these the closest to the Fair Isle material is assemblage D of late Givetian age, characterized by the appearance of *Grandispora protea* and *Chelinospora concinna*. The disappearance of *Densosporites devonicus* is not held to be of major significance as its replacement by *D. orcadensis* in the Orcadian sequence may be anomalous in view of the apparent synonymy which exists between the two species (see McGregor and Camfield 1976; McGregor 1979a and this paper).

Devonian spores described by Owens (1971) from Middle and Upper Devonian rocks of the Canadian Arctic Archipelago, suggest that broad similarities can be drawn, but his work is largely based on new species from a few horizons, and is of limited value for detailed comparisons.

Sanders (1968) described the miospores from an acritarch-dominated assemblage of Givetian age, with *Rhabdosporites langii* (and *R. parvulus*), *Geminospora tuberculata*, and examples of *Ancyrospora* spp. and *Velamispорites* spp. (*Perotrilites*).

#### *Comparisons with North African and the Middle-East Assemblages*

Massa and Moreau-Benoit (1976) described a series of miospore zones covering the Devonian strata of western Libya, and limited comparisons can be drawn with the Fair Isle succession. Palynozones 4 and 5 are the most similar, having *Auroraspora micromanifestus*, *Emphanisporites rotatus*, *Rhabdosporites parvulus* (*R. langii*), *Grandispora velata*, *Geminospora svalbardiae*, and *Samarisporites mediconus* in common, and these are dated as Couvianian and lower Givetian respectively.

#### *Comparisons with miospore assemblages from the Russian Platform*

*General comparisons.* Table 1 lists some miospore taxa from the Russian Platform together with their stratigraphical ranges, which are considered to be broadly comparable with taxa from Fair Isle. Comparability is variable, ranging from likely direct equivalence to part synonymy or closely similar. Some species, for example *Hymenozonotriletes protea*, can be referred to several western species.

In the compilation of Table 1 it was hoped to keep the stratigraphic information in the form of the local units used over the Russian Platform, but correlation difficulties made it impossible to construct a single table for the data, so that a more generalized scheme was necessarily produced. The placing of the Eifelian-Givetian and the Givetian-Frasnian boundaries is open to question, with some amendments having been made in certain areas. *Hymenozonotriletes punctomonogrammos* and *H. monogrammos* (Arkhangelskaya 1974), for example, are found in the Mosolovian and Chernoyarian beds of the Central and Eastern Russian Platform, and are part of the *polymorphos-monogrammos* zone which has many taxa similar to the Fair Isle material, but is placed in the Eifelian by Arkhangelskaya. A similar problem is seen in the Givetian-Frasnian beds of the Baltic region, where the Soviet workers draw the boundary at the base of the Gauja formation (e.g. Ozolin'a 1963), whereas recently compiled data (Westoll 1979 and pers. comm.), places it at the base of the Snetogor, which gives this succession great importance as being continuous across the Middle/Upper Devonian boundary and containing good vertebrate faunas. Unfortunately although this section appears to be well documented (e.g. Ozolin'a 1955, 1960a, 1960b, 1961, 1963; Kedo 1966) the miospore illustrations and descriptions are poor, making comparisons difficult. The compilation of data presented in Table 1 shows a Givetian age for the Fair Isle assemblages but it is impossible to give greater precision with this type of synthesis.

#### *Comparisons with zonal schemes from the Russian Platform*

Several zonal schemes have been published which cover the relevant stratigraphic interval, and specific comparisons are made in an attempt to give a more detailed correlation. Kedo (1966) produced a zonal scheme for the western part of the Russian Platform and although there are some taxa in common, it is very difficult to make a precise correlation, except to record an influx of *Archaeozonotriletes* (sensu Naumova = *Geminospora* spp.) in the upper part of the Givetian, which compares with Fair Isle, but contrasts with the Orcadian Givetian which does not contain *Geminospora*. This indicates either younger Givetian rocks in Fair Isle than in the Orcadian Basin, or the possibility of an ecological control (see below).

Raskatova (1969, 1974) has produced a more compatible scheme which again shows an influx of *Archaeozonotriletes* in the upper Givetian (zones IV to VIII) Vorbyeikian to Staryi' oskolian. *Hymenozonotriletes punctomonogrammos* Arkhangelskaya and *H. monogrammos* Arkhangelskaya are also present, but occur lower down in the uppermost Eifelian as well as the Givetian, so that the age assignment is not clear cut.

From the same horizons, Arkhangelskaya (1974) has also recorded these two species of *Hymenozonotriletes* as well as taxonomic equivalents of *Rhabdosporites langii*, *Densosporites devonicus*, *Grandispora protea*, and *Samarisporites* spp. These were compared with the Weatherall

TABLE 1. Comparative table of selected Soviet and western taxa occurring on Fair Isle. Records include likely synonymies, part synonymies, and close comparisons. Sources include Ozolin'a 1955, 1960a, 1960b, 1961, 1963, Kedo 1955, 1960, 1966, 1967, Chibrikova 1959, 1962, 1972, 1977, Chibrikova and Naumova 1974, Arkhangelskaya 1963, 1974, Naumova 1953, Andreeva 1962, Raskatova 1969, 1974, and Pokrovskaya 1966.

WESTERN TAXA	SOVIET COMPARISONS	EIFELIAN	GIVETIAN	FRANSIAN
Ancyrospora ancyrea	Archaeotriletes sincerus Kedo Archaeotriletes splendidus Kedo Archaeotriletes hamulus Naumova	•	• • •	•
Aneurospora greggsii	Retusotriletes verrucosus (Naumova in litt.) Kedo Retusotriletes punctatus Chibrikova Archaeozonotriletes nalivkinii Naumova		• • •	• •
Cirratiradites avius	Hymenozonotriletes punctomonogrammus Arkhangelskaya		•	
Cirratiradites sp. A	Hymenozonotriletes monogrammus Arkhangelskaya		•	
Densosporites devonicus	Hymenozonotriletes meonacanthus Naumova	•	•	•
Geminospora tuberculata	Archaeozonotriletes meonacanthus Nomen nudum Archaeozonotriletes tuberculatus Kedo Archaeozonotriletes plicata (Naumova in litt.) Kedo		• • •	
Geminospora svalbardiae	Retusotriletes parviammatus Kedo Archaeozonotriletes notatus Naumova Archaeozonotriletes rugosus Naumova		• •	• • •
Geminospora sp. A	Archaeozonotriletes visendus Chibrikova Archaeozonotriletes egregius Naumova Archaeozonotriletes tuberculatus var. aculeatus Raskatova Archaeozonotriletes acutus Raskatova Archaeozonotriletes visendus var. echinatus Chibrikova Archaeozonotriletes pensus Kedo Archaeozonotriletes lasius var. minor Naumova		• • • • • • •	• •
Geminospora sp. B	Archaeozonotriletes comptus Naumova Archaeozonotriletes comptus var. expletivus Chibrikova Archaeozonotriletes tuberculatus var. minor Kedo Archaeozonotriletes tuberculatus var. triangulatus Kedo		• • • •	
Grandispora naumovii	Archaeozonotriletes naumovii Kedo	•	•	
Grandispora protea	Hymenozonotriletes curticonicus Kedo Hymenozonotriletes ventosus Kedo Hymenozonotriletes proteus Naumova Hymenozonotriletes verus Naumova Hymenozonotriletes endemicus Chibrikova	• •	• •	
Grandispora velata	Hymenozonotriletes echiniformis Naumova Hymenozonotriletes longus Arkhangelskaya Hymenozonotriletes tener var. concinna Chibrikova Hymenozonotriletes proteus Naumova Grandispora velata (Richardson) Playford	• • • • •	• • •	
Rhabdosporites langii	Hymenozonotriletes facetus Arkhangelskaya Hymenozonotriletes polymorphus (Naumova) Kedo Archaeozonotriletes micromanifestus Naumova Hymenozonotriletes varius Naumova Rhabdosporites parvulus Richardson	• • • • •	• • • •	

Formation from Arctic Canada (Givetian), the Thurso and Eday Beds from the Orcadian Basin (Givetian), and the Achanarras Fish Bed (Eifelian-Givetian). The recent zonal scheme produced by Chibrikova and Naumova (1974) is not very detailed with regard to specific taxa, and is largely restricted to generic distribution. The appearance of *Archaeozonotriletes* is considered significant, and is used as a marker for the Givetian stage. The zonal scheme produced by Naumova (1953) is difficult to apply, as the taxa are not often placed in a detailed zonal scheme, but in broad categories

such as Middle or Upper Devonian. The Fair Isle assemblages fit best into the Givetian and Frasnian groups.

A compilation of these occurrences has been presented by Andreeva (in Pokrovskaya 1966) and, as indicated, uses Chibrikova's (1962) and Naumova's (1953) work. The significant occurrence of *Archaeozonotriletes* (= *Geminospora*) with subordinate *Hymenozonotriletes* is used as a marker for the Givetian stage. The spores recovered by Chibrikova (1962) from the Vorobyevkian of Western Bashkiria contain several species which are similar to the Fair Isle assemblages, with examples such as *Archaeozonotriletes comptus* var. *expletivus*, *A. meoncanthus*, *A. visendus*, and *A. egregius*.

	Sample No.	Zonate	Pseudo-saccate	<i>Geminospora</i> spp. and <i>Aneurospora</i>	<i>Hystricosporites</i>	<i>Aneurospora</i>	Others
Bu Ness Group	Fair 24	6	14	39	2	20	19
	Fair 28	4	39	3	0.5	30	23.5
	Fair 33	2	19	15	3	53	8
Observatory Group	Fair 36	8	47	11	2	13	19
	Fair 67	5	37	2	27	27	2
Ward Hill Group	Fair 66	6	33	36	—	21	1
	Fair 64	19	35	2	5	38	1

TABLE 2. Relative proportions of major miospore types from Fair Isle. The figures are percentages of numbers of each group from 150 total counts.

### Ecological considerations

An ecological control on the distribution of some Devonian miospores has been speculated by several authors (e.g. Streele 1967; Richardson 1965, 1967, 1969), and the example cited is usually that of *Geminospora* spp. (*Archaeozonotriletes* of Soviet palynologists). These miospores are thought to be dispersed from plants growing on and around the lower flood plain and marginal marine areas, whilst miospores from the bifurcate and pseudosaccate zonate groups are more continental in aspect and related to upper flood plain and possibly lacustrine deposits. The assemblages from Fair Isle are relevant to this discussion as they often contain abundant *Geminospora* spp. (fluctuating from 39% to 2%, see Table 2), in what appears to be a true internal basin facies. The presence of *Svalbardia scotica* (Chaloner 1972) in the Bu Ness Group is also significant, because other species are known to contain *in situ* spores of *Geminospora* and *Aneurospora* (see Allen 1980), suggesting that their origin is local. The occurrences are also not restricted in the Fair Isle succession (see text-fig. 6), being found in the minor argillite horizons (?lacustrine deposits) of the Ward Hill Group (alluvial fan deposits) as well as the overbank deposits of the Bu Ness Group. This distribution contrasts strongly with that of Richardson (1965, 1967, 1969), who noted an absence of *Geminospora* from the lacustrine and fluvial deposits from the Orcadian basin lying to the south. A possible explanation is that the time difference between the Orcadian and Fair Isle deposits is sufficient to allow the migration of an 'Archaeozonotriletes' microflora from the Russian Platform, where it occurs in lower Givetian deposits (Raskatova 1974) contemporaneous with the Orcadian Basin. A less appealing hypothesis is that the Fair Isle lacustrine and fluvial deposits were sustained by permanent water flow, giving more equable conditions than those in the Orcadian Basin, and similar to conditions seen on delta tops or marine margins, where *Geminospora* is known to thrive (see Becker *et al.* 1974). These authors describe in detail the distribution of *Aneurospora greggsii*, and suggest it is not restricted by ecological factors in their environment studied, which unfortunately do not include lacustrine or alluvial fan facies. It



seems that this conflict between an edaphic or stratigraphic control will not be resolved without further detailed palaeoecological studies of this type.

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